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Technical Report 146

CRITICAL ASSESSMENT OF HABITAT FOR RELEASE OF MAUI PARROTBILL

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ABSTRACT

The Maui Parrotbill Working Group and Hawai‘i Forest Bird Recovery Team have identified key objectives toward recovery of the critically endangered Maui Parrotbill (*Pseudonestor xanthophrys*). Among these are the development of a captive propagation and release program and the identification of habitat requirements for parrotbill. The Manawainui rainforest of Haleakalā National Park was identified as one of three potential future release sites. Research was conducted on the habitat use of the Maui Parrotbill in Manawainui to determine if the existing habitat was suitable for release of captive-bred birds. The primary goal of this study was to provide a quantitative assessment of habitat that could guide future management decisions regarding potential reintroductions of this species. I studied habitat suitability for Maui Parrotbill at 21 10-hectare sites (10 used, 11 unused) in mixed ‘ōhi‘a-koa (*Metrosideros polymorpha-Acacia koa*) forest in Manawainui from February-August 2005 and January-August 2006. A combination of bird and vegetation surveys were utilized to compare vegetation parameters between used and unused areas at different spatial scales of macrohabitat (home range) and microhabitat (foraging site). I found that parrotbill occurred in 49% of the 210 hectares of habitat surveyed for birds and vegetation. Parrotbill exhibited non-random habitat use at multiple spatial scales. At the macrohabitat scale, vegetation structure and composition differed significantly between used and unused areas. Parrotbill were associated with areas typified by large diameter trees and higher densities of understory, subcanopy and canopy vegetation layers. Significant indicator species of parrotbill habitat use at the macrohabitat scale were ‘ōlapa (*Cheirodendron trigynum*), kawa‘u (*Ilex anomala*), and ‘alani (*Melicope* spp.). At the microhabitat scale, parrotbill selected foraging sites non-randomly and were most influenced by overall species composition. Birds selectively foraged on ‘ōlapa, ‘alani, koa, and ‘ākala (*Rubus hawaiensis*) in disproportion to their availability. Overall vegetation structure did not differ significantly between used and unused foraging plots, however parrotbill did selectively forage on smaller diameter trees and used the subcanopy and canopy more than expected. These data highlight the importance of diverse, well developed forest for this species and have important management and conservation implications.

INTRODUCTION

BACKGROUND

Reintroduction of captive-reared birds to augment existing bird populations in the wild is a major emphasis of current avian recovery efforts in Hawai‘i (Banko et al. 2001, Tweed et al. 2003). Conservation and restoration of habitat for the benefit of avian species is specified as a major recovery objective in the current Recovery Plan for Hawaiian Forest Birds (USFWS 2006). Understanding which aspects of habitat are most critical in determining site occupancy for forest bird species is imperative if restoration efforts are to be effective in guarding against further extinctions. In the past, recovery efforts in Hawai‘i for many birds of rarity, such as the Po‘ouli (*Melamprosops phaesoma*), were initiated when population levels were already too low to accurately assess and identify limiting factors (Groombridge et al. 2003). Therefore, it is essential to initiate studies on aspects of habitat that may be limiting for endangered birds before they become too rare. Understanding habitat factors and determining the suitability of potential release areas is an important step in the development of effective conservation strategies, particularly for endangered species (Conway and Martin 1993, Pasinelli 2000).

The Maui Parrotbill (*Pseudonestor xanthophrys*) (population 500 ± 230, 95% CI individuals) is among the most threatened of the remaining Hawaiian honeycreepers (Scott et al. 1986), reproducing at a rate of only one young/year (Simon et al. 2000). It is now restricted to the island of Maui, where it occupies approximately 5% of its original range (Scott et al. 1986). Parrotbill maintain year-round all-purpose territories, a characteristic common to many insectivorous Hawaiian honeycreepers (Pratt et al. 2001b). Recently, this medium-sized (20-25 g) olive-green honeycreeper has become a target for conservation efforts on the island of Maui because it is the only endangered insectivore that may still benefit from recovery measures. Two other endangered, insectivorous honeycreepers on Maui that historically had similar habitat requirements, the Po‘ouli and the Nukupu‘u (*Hemignathus lucidus*), may be extinct. Both species foraged on invertebrates from woody trees, shrubs, and/or epiphytic material in similar habitat types as the Maui Parrotbill (Perkins 1903, Scott et al. 1986, Baker 2001). Their decline suggests that parrotbill may be subject to the same threats. The Maui ‘Alauahio (*Pareomyza montana*) the only other native insectivore on Maui, is not endangered and is frequently sympatric with Maui Parrotbill (Baker and Baker 2000). ‘Alauahio however, occupy a slightly different foraging niche which may account for their more extensive range.

Since the early 1900s, the Maui Parrotbill has continued to persist in low numbers in the upper elevation montane rainforests of the dormant Haleakalā volcano (Scott et al. 1986, Simon et al. 1997). However, fossil evidence suggests that parrotbill existed in the dry lowland and mesic leeward forests of Maui prior to human contact (Olson and James 1982a, Scott et al. 1986, Mountainspring 1987) (Figure 1). A variety of dry and mesic forests once occurred from tree-line to sea level on the leeward side of the island of Maui. By the late 1890s most of these forests, some composed of the dominant canopy tree koa (*Acacia koa*), had been destroyed (Scott et al. 1986). Perkins (1903) and Henshaw (1902) noted that parrotbill frequently foraged in koa; currently this canopy tree is now greatly diminished. It is widely believed that logging of this valuable wood decreased much of the habitat available for parrotbill (Olson and James 1982b, Scott et al. 1986, Simon et al. 2000). This habitat loss, as well as the introduction of avian disease to which native birds lacked resistance (Atkinson et al. 1995, van Riper and Scott 2001),

may have contributed to the contraction of the parrotbill's historical range. Parrotbill currently persist in upper-elevation ʻōhiʻa (*Metrosideros polymorpha*) rainforests at densities of 10 birds/km^2 (USFWS 2006). Research in the 1990s indicated this species was at carrying capacity in its current range and further suggested that this habitat was only marginally suitable for the species (Simon et al. 2000, Pratt et al. 2001b). No recent studies have validated this. Ongoing research occurs in Hanawī, a core activity area for Maui Parrotbill, but the forests of Waikamoi and Manawainui at the edge of this species' range have been little explored.

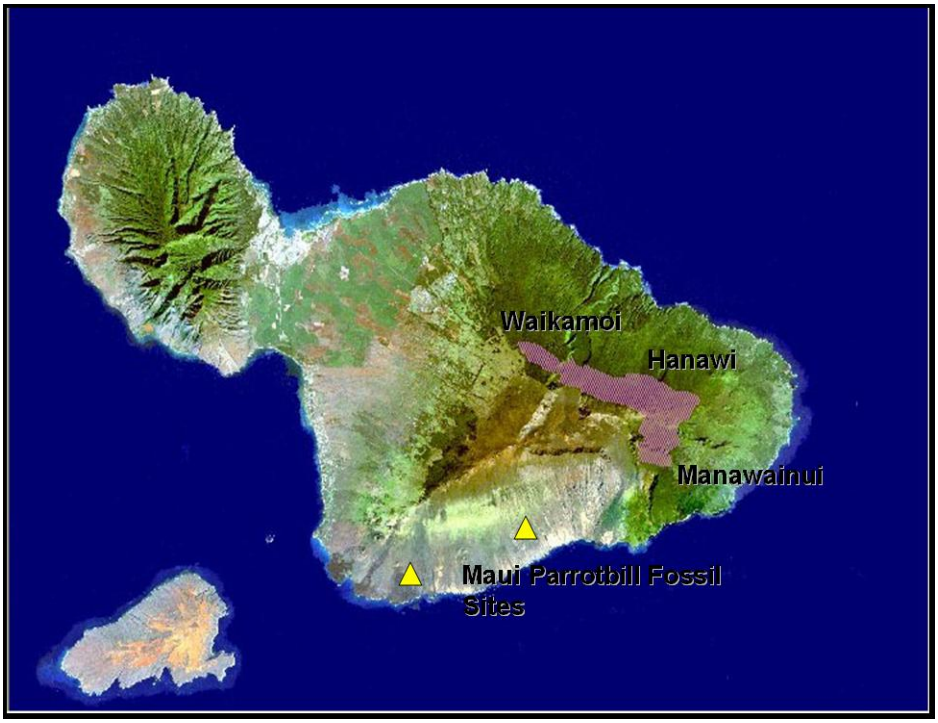


Figure 1. Current and historical range of Maui Parrotbill on Maui (adapted from the USGS-Pacific Basin Information Node website).

Mountainspring (1987) identified lack of suitable habitat as the primary threat for Maui Parrotbill. The protection, acquisition, and restoration of parrotbill habitat in areas of its historic range are high priorities in the Revised Recovery Plan for Hawaiian Forest Birds. The State of Hawaiʻi's Division of Forestry and Wildlife is currently committed to the long-term restoration of remnant koa forests that exist in portions of historic parrotbill range, with the ultimate goal of reintroducing captive-reared birds to the leeward side of Maui (Scott Fretz, pers. comm.). However, reintroductions and the acquisition and subsequent restoration of critical habitat are costly and time consuming ventures. Before new areas can be made usable for parrotbill, it is important to determine which attributes of its habitat in occupied areas are most important. Previous researchers have provided insight into parrotbill breeding biology, morphology, and territoriality (Lockwood et al. 1994, Simon et al. 1997, Simon et al. 2000, Pratt et al. 2001b). However, research on Maui Parrotbill habitat use has been limited. General assessments of Maui

Parrotbill distribution and habitat use were documented in the 1980s and suggested a preference for upper montane ʻōhiʻa and ʻōhiʻa-koa forest (Scott et al. 1986). Mountainspring (1987) found parrotbill foraged extensively in the forest understory and subcanopy and made a majority of prey captures on ʻōlapa, ʻōhelo, pilo, ʻalani, and kanawao. Perkins (1903) also noted heavy use of koa and ʻalani, suggesting the importance of these plants. These early investigations of habitat use occurred prior to intensive management for feral ungulates. Recent quantitative assessments of Maui Parrotbill habitat requirements are lacking. A quantitative approach, may identify limiting factors in habitat that may qualitatively appear suitable (Fretz 2002).

The evaluation of habitat is a crucial first step toward implementing a sound wildlife management or monitoring program (Wiens and Rotenberry 1981a) and rigorous quantification of habitat should precede any reintroduction program (Armstrong and McLean 1995). The reintroduction guidelines set forth by the International Union for the Conservation of Nature and Natural Resources stress the importance of evaluating the suitability of potential habitat (IUCN 1998) for reintroductions and translocations. Successful reintroduction and translocation projects should carefully consider factors such as habitat quality and quantity at the release site, numbers of individuals released, and the relationship of the release site to the animal's historic range (Wolf et al. 1998). Reintroductions frequently fail because of immature or inadequate habitat, or because key factors responsible for a species' initial extirpation have not been adequately identified and remedied (Armstrong and Ewen 2002). Incorporating a scientific approach with hypothesis testing can greatly enhance the outcome of potential reintroduction projects by more accurately identifying limiting factors (Armstrong and McLean 1995, Seddon et al. 2007). This study highlights the merit of using this method to quantitatively assess habitat as a precursor to the potential reintroduction of an endangered bird.

Research Objectives

The Manawainui forests of Haleakalā National Park were previously identified by the Maui Parrotbill Working Group as one of three potential release sites for future Maui Parrotbill reintroductions (Figure 2). Subsequently, this project was initiated to assist the National Park Service in determining the suitability of Manawainui as a release site for captive-bred parrotbill. Initial bird surveys by Stemmerman (1976) and the Hawaiʻi Forest Bird Survey (Scott et al. 1986) failed to confirm the presence of parrotbill in this area. However, in the early 1990s following ungulate management efforts of Haleakalā National Park, biologists started to detect parrotbill locally in low numbers (Reynolds and Snetsinger 2001, Haleakalā National Park unpubl. data). It is uncertain if these detections were a direct result of management efforts, better census data, or both. Park biologists, continue to conduct yearly forest bird surveys on U. S. Fish and Wildlife Service transect 18 which is oriented north to south through the Manawainui area. Until recently, parrotbill distribution from east to west in this area was not known. To better understand the relationship between parrotbill and its habitat use, the main objectives were to (1) determine the distribution of parrotbill in Manawainui, (2) determine which proximate vegetative factors make habitat suitable for Maui Parrotbill, and (3) determine the effect of scale on habitat selection by this species.

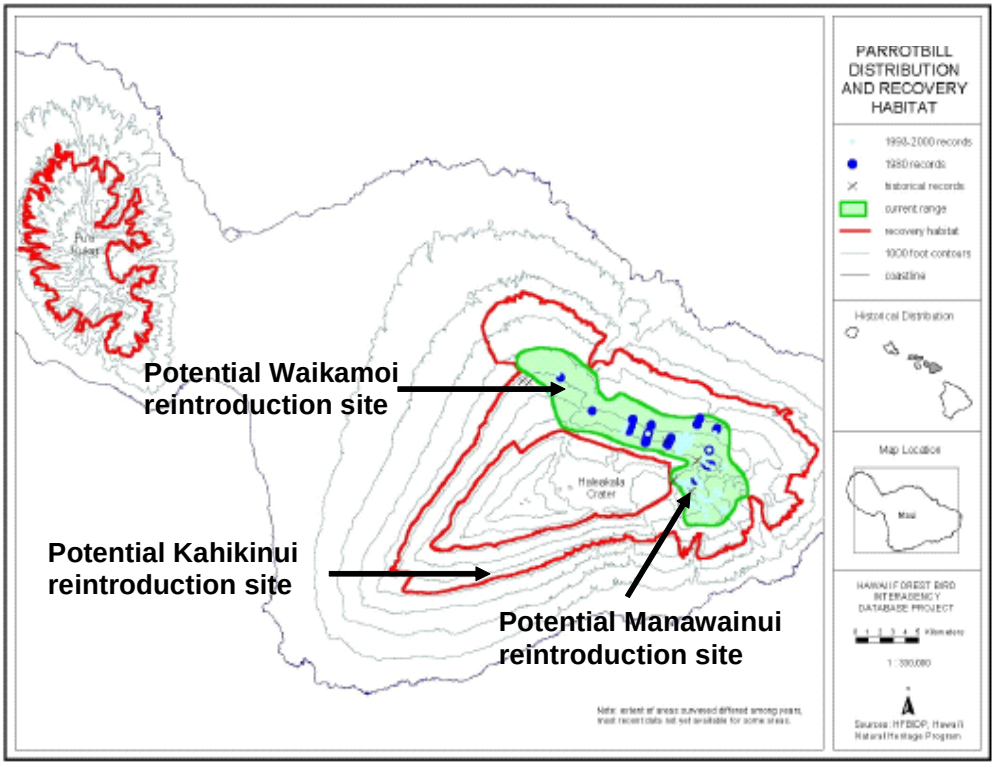


Figure 2. Potential reintroduction sites for Maui Parrotbill on East Maui. Current habitat is in green; proposed recovery habitat is denoted by red boundary (adapted from USFWS 2006).

The identification of habitat variables important to Maui Parrotbill could guide the selection of future release sites and the restoration needs of these areas. Understanding resource use is necessary to determine the relationship between an organism and its habitat (Heglund 2002). Vegetation structure and composition are the primary proximate factors that determine where and how a species uses its resources (Block and Brennan 1993) and quantifying the relationships between parrotbill and vegetation are critical to its recovery. Vegetation attributes influence the distribution and abundance of birds either directly, such as for nesting sites, or indirectly through the provision of food resources (Wiens and Rotenberry 1981a, Rotenberry 1985, Luck 2002). Thus, understanding how a species uses certain habitat features such as vegetation is useful for communicating the physical significance of these attributes to resource managers and scientists by facilitating more effective design of natural area reserves and appropriate vegetation components.

Because key habitat variables will be most accurately identified when studied at the appropriate scale (Orians and Wittenberger 1991), hierarchical assessments of habitat variables at different scales have become essential to understanding avian habitat use and needs (Kristan and Scott 2006). Single-species assessments of habitat use at several increasing scales of resolution can be especially useful because they may provide more direct insight as to why a species is selecting for a particular habitat type (Cody 1985, Orians and Wittenberger 1991, Bergin 1992, Luck

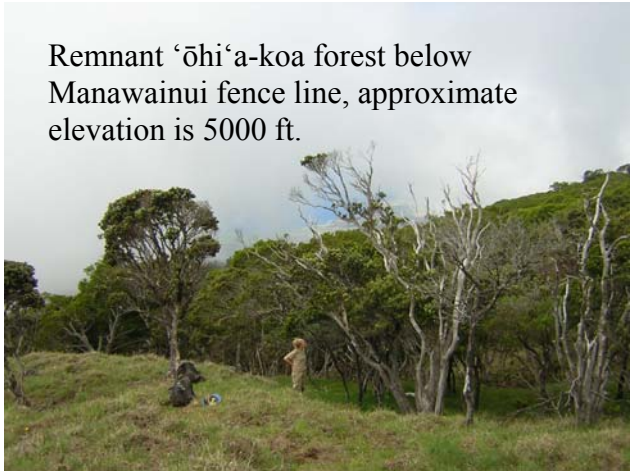
2002, Hobbs 2003). Wiens and Rotenberry (1981b) found that the initial occupation of habitat in shrubsteppe birds was driven by vegetation structure and that within site distribution patterns were further refined by their association with plant species composition. The simultaneous assessment of the relative importance of gross or "coarse" habitat features, in an area as well as those obtained by watching specific behavior such as singing or foraging has predictive significance because it allows us to determine which habitat variables are most important and at what scale (Bibby et al. 2000). For example, Luck (2002) studied habitat use by Rufous Treecreepers (*Climacteris rufa*) in Australia at four spatial scales and found birds prefentially selected habitat based on different vegetation variables at each scale. At the broadest or landscape scale, birds preferred to settle in particular forest-type. They then selected territories and foraging sites based on the presence of scale-specific habitat variables.

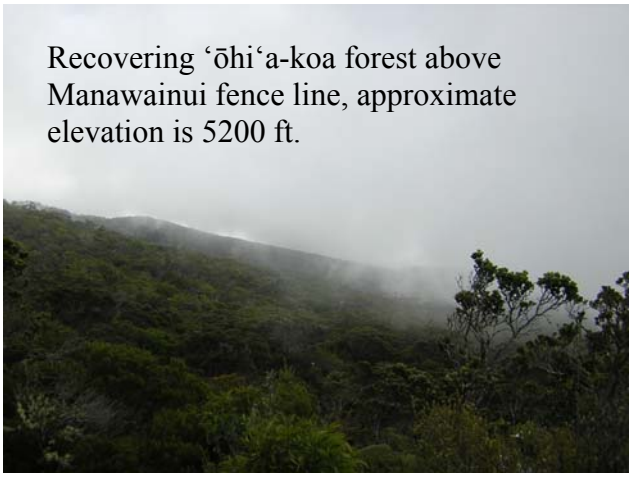
To explore the relationship between vegetation structure and composition and Maui Parrotbill habitat use, I asked the following questions at three spatial scales of increasing resolution (home range, foraging site, and plant species; see Johnson 1980) in used and unused sites within the same general habitat type: (1) do differences in vegetation structure and/or composition across the forest influence patterns of home range use by parrotbill? (2) do parrotbill preferentially select foraging sites based on certain structural or compositional aspects of the vegetation? and (3) is use of certain plant species, vegetation strata and tree size class by parrotbill proportional to availability throughout the study site?

METHODS

STUDY SITE

This study was conducted in Manawainui (20°41'43" N, 156°7'59" W), a 526-hectare (1300-acre) parcel of Haleakalā National Park at the southeastern-most edge of the East Maui rain forest (Figure 3). Manawainui has been recovering from feral ungulate damage for approximately 24 years; longer than most other sites on Maui. As a result of this recovery and its proximity to historic parrotbill range, it is an area of forest being considered for future reintroductions of captive reared Maui Parrotbill. It is an ecotone between wet and dry forest, dominated by wet ʻōhiʻa forest, mesic koa and mixed ʻōhiʻa-koa forest.


Remnant ʻōhiʻa-koa forest below Manawainui fence line, approximate elevation is 5000 ft.


Recovering ʻōhiʻa-koa forest above Manawainui fence line, approximate elevation is 5200 ft.

Gross vegetation cover classes have been previously documented by Jacobi (1989). The topography in the area is extreme, divided by gulches and streams with an average slope of > 30%. Environmental and anthropogenic disturbance in the area has included degradation by feral goats (*Capra hircus*) and pigs (*Sus scrofa*), and invasion by weeds (Peterson 1976, Loope et al. 1992). Interestingly, this forest was initially isolated by lava flows which inundated nearby Kaupō Gap and Kīpahulu Valley and may be much older than the surrounding environs due to this isolation (Peterson 1976). Climactically the area is dynamic, with high precipitation (i.e., orographic rains and mist) in excess of 5,000 mm per year. Rainfall tapers off from east to west, marking the transition from the windward to leeward sides of the island. Manawainui is intensively managed to control feral ungulates, and marks the edge of current parrotbill range on southwest Haleakalā.

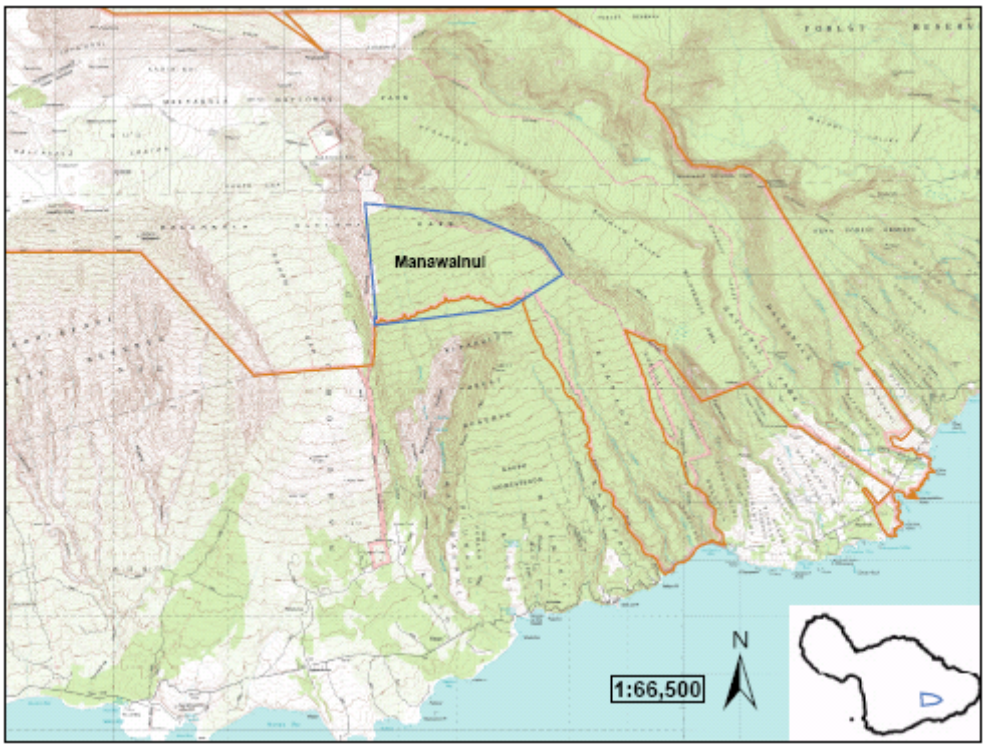


Figure 3. Overview of Haleakalā National Park with inset of Manawainui area.

All work was conducted above 1585m elevation (5200 ft). Therefore, the effect of disease as a confounding factor on parrotbill distributions was minimized. Conducting work at this elevation also reduced the spread of invasive weeds that occur at lower elevations in Manawainui because elevation limits natural recolonization of some weeds in this recovering forest. To assess whether changes in vegetation across the habitat gradient in Manawainui were affecting parrotbill distribution and use, simultaneous surveys of vegetation, birds, and bird foraging behavior were conducted over the course of two field seasons from February 2005 to August of 2006. This spans most of the known breeding season for parrotbill (Simon et al. 1997) and should have

reflected the time of year when resources would be most critical for the reproduction and survival of young.

I selected 10-hectare areas as my study unit in which to conduct vegetation sampling and foraging observations as a conservative estimate of home range size for the parrotbill. Home ranges for Maui Parrotbill average 2.3 hectares (5.7 acres) in size (Simon et al. 2000, Pratt et al. 2001b). As the birds in this study were not banded, each 10–hectare home range (used) or "pseudo home range" (unused) helped to maintain a level of independence throughout the course of the study. Using Geographical Information Systems technology, I superimposed a grid partitioned into 10-hectare units across the area, and assigned each 10-hectare survey area a unique letter identifier (Appendix 1). The initial survey grid included 27 ten-hectare study areas. Subsequent vegetation sampling was conducted in 22 of these 10 hectare areas in accessible areas where parrotbill occurred and in areas where they were absent (Figure 4).

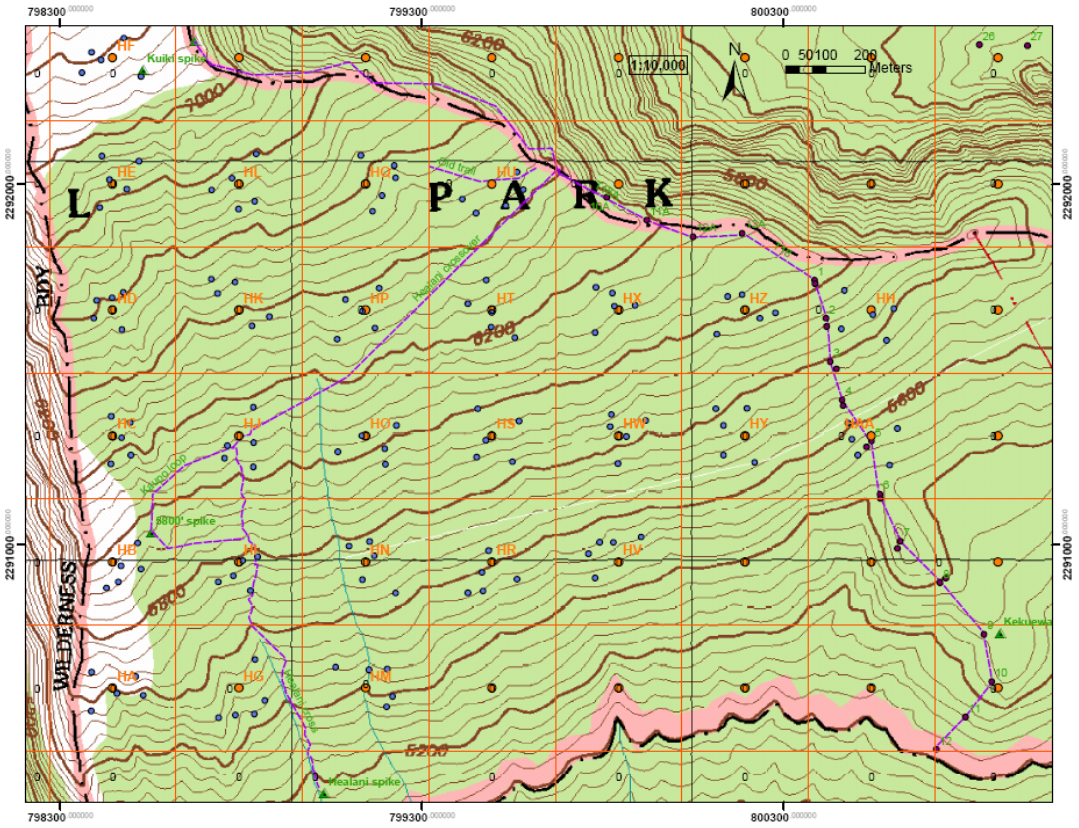


Figure 4. Detailed overview of Manawainui study site with lat-long references. Blue dots indicate (0.04 ha) vegetation plots and orange gridlines with letters denote each 10 ha area surveyed for Maui Parrotbill.

BIRD SURVEYS

Spot-mapping techniques (Bibby et al. 2000) were used to assess the density and distribution of parrotbill across the study site. I searched 27 10-hectare areas from February 2005-August 2005,

and January 2006-August 2006. Full vegetation and bird surveys were conducted only in 22 of the 27 survey areas because treacherous topography made surveying all areas difficult. To maximize the potential of encountering parrotbill, I attempted to survey each 10-hectare area for at least four hours each month; however, this was not always possible due to poor weather conditions. Selection of survey areas was arbitrary, but without preconceived bias. Survey times were alternated (morning vs. afternoon surveys) to increase encounter rates with individuals active at only certain times of the day. Observers were rotated among home ranges to prevent bias. Audio playback equipment was used to increase the chance of detecting birds in new areas. Observers moved around each 10-hectare area during each 4-hour survey period, as is done in standard spot mapping surveys (Bibby et al. 2000). If a parrotbill was observed foraging during a survey, the observer stopped to conduct foraging observations and microhabitat analysis. Individual birds were assigned ID numbers which associated them to the nearest survey area in which they were found. In addition to location, individuals were further identified by unique coloration and/or vocalizations. Parrotbill are sexually dimorphic and singing is unique to males (Simon et al. 1997), thus birds were sexed based on vocalization and obvious dimorphisms such as bill size and plumage coloration. I was unable to search many of the areas below 1646m elevation due to treacherous terrain and the possibility of spreading incipient weeds. I did not consider these to be priority areas however, due to the prevalence of avian malaria at lower elevations (Atkinson et al. 1995).

VEGETATION SAMPLING-MACROHABITAT

I selected a random sample, of 0.04-hectare (11.3 m radius) circular plots stratified by each 10-hectare survey area across the Manawainui study site, $n = 107$ (Figure 4). These plots spanned the east to west habitat reflecting the structural and compositional heterogeneity of the area as suggested by Noon (1981). Due to habitat heterogeneity, I randomly selected five replicates in each home range using the random sampling extension in ArcGIS. UTM coordinates of sampling areas were uploaded into Garmin GPS units to locate plots in the field. I used the methods of James and Shugart (1970) as modified by Noon (1981) to sample habitat data at each plot. These variables were comprised of slope, elevation, percent canopy and ground cover, canopy height, shrub and tree densities (in 3 different size classes); canopy, subcanopy, and understory density, and plant species (Table 1).

I identified all woody and herbaceous plants within each 0.04-hectare plot concurrent with stem counts to ascertain relative abundance of plants throughout the study area. Most woody plants were identified to species. Unidentified specimens were brought back to Haleakalā National Park (HALE) headquarters for identification by National Park Service botanists. Specimens were deposited in the HALE herbarium. I attempted to identify all plants to species; however some plants could be identified only to genus due to morphological heterogeneity and hybridization (P. Welton, pers. comm.).

Table 1. Description of habitat variables measured for each 0.04 hectare plot in used and unused areas.

Habitat Variable	Abbreviation	Description
Percent canopy closure	CanCo	Estimated as the presence or absence of leaves sighted through densitometer along two 22m transects in each plot
Percent ground closure	GrnCo	Same as above but for ground cover
Canopy height	CanHgt	Estimated as the mean canopy height for each plot using a clinometer
Density of small trees	DBHsmall	Number of trees per home range (3-15 cm dbh) measured using a forester's diameter tape.
Density of medium trees	DBHmed	Number of trees per home range (16-53 cm dbh)
Density of large trees	DBHlarge	Number of trees per home range (≥ 54 cm dbh)
Density of shrubs	Shrubtls	Total woody shrub stem count at breast height < 3 cm dbh, estimated for two 22m transects in each plot
Canopy density	Cantot	Index of species abundance ≥ 12-m tall according to Braun-Blanquet cover abundances
Subcanopy density	Subcan	Index of species abundance 5-12-m tall according to Braun-Blanquet cover abundances
Understory density	Under	Index of species abundance 0-5m tall according to Braun-Blanquet
Plant Species		Counted and identified to genus and species
Slope		Estimated using a clinometer
Elevation		Estimated using an altimeter

DATA ANALYSES-MACROHABITAT

All data were input into Microsoft Access 2000 and proofed for errors. Tree height data were computed from field-based clinometer readings and all heights converted into meters. Plant species stem counts were converted to stems per hectare. Due to the large amount of data collected, it was necessary to reduce many of the original variables into smaller subsets of manageable data for further analysis. For example tree size class data were originally collected in nine different dbh size categories but was later condensed into three size classes (small, medium, large) for easier interpretation. The data collected from the original 107 vegetation plots were expressed as mean values for the variables in each of the 22 10-hectare areas sampled. Due to incomplete data, survey area HA (n = 3) was dropped from further analyses, leaving a final sample of 104 plots in 21 10-hectare areas. A complete list of vegetation plots sampled with UTM coordinates and mean values for the variables measured can be found in Appendices 2 and 4. Data were assessed for strong outliers (cut off of > 3 SD) and normality using frequency distributions, normal probability plots and the Shapiro-Wilkes test. I did not detect any strong outliers, for structure or floristics, however the data were non-normal and heteroscedastic. I assumed those variables that were univariate normal approximated multivariate normality (McGarigal et al. 2000). All descriptive and statistical analyses were performed in Systat 11 and PC-Ord version 5.

I used multi-response permutation procedure (MRPP), a non-parametric multivariate method, to test for significant differences between used and unused areas; $n = 21$ (used = 10 vs. unused = 11). MRPP is a distribution free test similar to discriminant analysis (DA) and multivariate analysis of variance (MANOVA) that tests for differences between groups but with relaxed assumptions. The MRPP *T*-test statistic is based on numerous permutations of the data itself, instead of a predetermined distribution (Mielke 1984, Mielke and Berry 2001). I used the Sorensen (Bray-Curtis) distance measure with the recommended weighting of n/sum (n), as it is sensitive to heterogeneous data (McCune and Grace 2002). The data matrices were rank-transformed to account for heterogeneity of the data set. I followed this procedure for both structure and floristics and ran separate MRPP tests for each.

I used Nonmetric Multidimensional Scaling (NMS), a robust, iterative ordination technique to graphically represent the degree of dissimilarity between the used and unused areas. NMS avoids the assumptions of linearity used in other ordination methods (Kruskal 1964, Mather 1976). In addition, NMS differs from other ordination procedures in that the assignment of axes is arbitrary. I used autopilot mode in PC-Ord with the Sorensen (Bray-Curtis) distance measure, and ran 250 runs of real data and 250 runs of random data. Dimensionality of the data set was assessed graphically by a scree plot, by seeking a low stress solution and by assessing Monte Carlo *p*-values ($p < 0.05$) for significance. I followed this procedure for broad patterns in both vegetation structure and floristics and used the methods below for more detailed analysis of specific variables in each group.

Vegetation structure

The final group of ten habitat variables retained for further analyses of vegetation structure was based on biological relevance and included: percent ground cover, percent canopy cover, mean canopy height, small, medium, and large tree totals, sub-canopy, canopy, and understory foliage density indices and shrub stem totals. Since the variables were expressed using different units, variables were standardized by column totals.

Because MRPP does not distinguish between those variables contributing most to group separation, Discriminant Analysis was used in a descriptive mode to identify what variables might be affecting group membership of used and unused areas. Values were screened for normality separately for each group of used ($n = 10$) and unused ($n = 11$) areas. Medium trees (DBHMED) and canopy densities (CANTOT) were log transformed to meet assumptions of normality and homogeneity of variance. Multicollinearity was assessed using scatter plot matrices and tested for significance using the Pearson correlation coefficient with an $r \geq 0.7$ as criterion for deleting a variable (Tabachnick and Fidell 1996). The final seven variables included density of the understory, subcanopy, and canopy layers, and the number of small, medium, and large trees and shrubs.

Floristics

Relative abundance of all woody species was calculated separately for trees and shrubs because I wanted to assess whether or not certain shrubs or tree species might be particularly influential. I considered as shrubs all woody species with a diameter at breast height (dbh) less than 3 cm and trees anything over 3 cm. I also estimated the relative abundance of ferns and forbs; however these data were omitted from further analysis because of its unlikely contribution to parrotbill

habitat use. Those other woody species that occurred in < 5% of the sample units were also omitted from further analyses. I retained a total of 10 plants for my final analyses which included: ʻalani (*Melicope* spp.), kanawao (*Broussaisia arguta)*, kawaʻu (*Ilex anomala*), koa, kōlea (*Myrsine* spp.*)*, ʻōhelo (*Vaccinium calycinum)*, ʻōhiʻa, ʻōlapa (*Cheirodendron trigynum),* pūkiawe (*Leptecophylla tameiameiae)*, and standing dead trees.

Data were non-normal and heteroscedastic, therefore non-parametric analyses were used. I ran an indicator species analysis to identify those species that were most useful in separating used from unused areas (Dufrene and Legendre 1997). This procedure calculates the proportional abundance of a species in one group versus its abundance in all groups. An indicator value is obtained for each species, ranging from 0 (no indication) to 100 (perfect indication). Statistical significance is evaluated by a Monte Carlo randomization test for each species ($p < 0.05$).

Diversity

I assessed diversity between all used and unused areas for trees, shrubs, and trees and shrubs combined. Shannon Wiener (H) and Simpson's (D´) diversity indices were calculated for all areas using PC-Ord and tested for significance using separate Mann-Whitney U tests for those species used in the MRPP analyses. Finally I tested for differences in overall species diversity including those species that occurred in < 5% of the survey areas.

VEGETATION SAMPLING-MICROHABITAT

Within each used 10-hectare survey area, detailed foraging observations on individual parrotbill were collected following the standard behavior classification scheme of Remsen and Robinson (1990). I also noted bird age and sex when possible. Since parrotbill are rare and encounters infrequent, I spent as much time watching a foraging bird as possible, recording the total observation time for each individual. Only initial observations were included in the analyses however, to minimize the effects of autocorrelation. In addition to collecting behavioral data, vegetation data was collected on foraging microsites or "patches". Upon encountering a parrotbill, bird-centered vegetation plots were selected by marking the first location it was seen foraging (Larson and Bock 1986). The first foraging observation point was identified as the point at which the first foraging maneuver was observed, after waiting ten seconds to remove any observer imposed bias.

Data on vegetation parameters were collected at several scales of increasing resolution using the first foraging location as the center reference point from which to collect additional data. In addition to collecting data at this point, I also collected data at two other scales of 1-m and 2-m radii. The 1-m radius might influence parrotbill foraging at the inner portion of a patch while the 2-m radius might represent the maximum extent of the foraging patch that the bird might spend time in before moving somewhere else in its home range.

I collected information on a series of vegetation variables that may be important to parrotbill foraging behavior, based on a review of pertinent literature (Table 2). At the point of initial contact, I identified the plant species and determined its height, as well as the bird height above ground (using the same height tier classes as for macrohabitat), substrate type (foliage, wood, and berries), tree size class, and branch size (small, medium, large).

In the 1-m radius, I collected data on foliage density and bark surface area, using one of six categories (Remsen 1985), and the number of branches approximating the number of perches parrotbill could have used.

At the broadest scale (i.e., the 2-m radius), I recorded data on species and the foliage density of each vertical vegetation class (i.e., canopy, subcanopy, understory) according to the Braun-Blanquet cover abundance scale (Braun-Blanquet 1932) and percent canopy and ground cover, using a densitometer.

I then measured these same variables (with the exception of bird height and substrate type) at the same scales at randomly located plots 20 m away (following methods of Moser et al. 1990, VanderWerf 1993). Habitat variables were measured in 36 used and 36 random plots at these three different scales of resolution in nine of the home ranges parrotbill were actively using.

Table 2. Summary of habitat variables measured for microhabitat at foraging sites and random sites.

Habitat Variable	Scale	Description
Plant Species	0,1,2m	counted as presence/absence
Plant Height	0m	estimated in meters
Canopy Height	0m	estimated in meters
Branch Size (cm)	0m	circumference estimated in cm using Maui Parrotbill as a "ruler"
Tree dbh (cm)	0m	estimated using a forester's diameter tape
Branch Count	1m	counted all branches in the same plane as first foraging maneuver
Foliage density index	1m	estimated in the same plane as the first foraging maneuver
Bark surface area index	1m	estimated in the same plane as the first foraging maneuver
Vertical Ht tier index	2m	estimated for understory, subcanopy, and canopy
Canopy Cover (%)	2m	estimated using a densitometer
Ground Cover (%)	2m	estimate using a densitometer

0m is the point at which the bird's first foraging maneuver was observed

1m is a 1-m radius extending out from the first point of observation

2m is a 2-m radius extending out from the first point of observation

DATA ANALYSES-MICROHABITAT

Data were screened for normality, outliers, and homogeneity of variance using the same criterion as for macrohabitat, for each of the three microhabitat scales (0-m, 1-m, and 2-m). The data for structure and floristics at all three scales were highly non-normal and heteroscedastic. Monotonic transformation of individual variables had little effect on normality; therefore I utilized non-parametric multivariate methods to test for significant differences in forest structure and floristics between plots. Structural data measured on different scales or units was standardized by column totals. Species data was represented as presence/absence and standardization was unnecessary. To test the hypothesis of no difference between used and random foraging plots, I used PerManova, a “distribution free” significance test for balanced study designs (Anderson 2001). The unit of analysis was the foraging site and not the individual. PerManova calculates an *F* test

statistic similar to MANOVA; however, the test statistic is evaluated for significance by running a series of randomized permutations of the data. I followed the suggestions of Anderson (2001) and ran 1000 permutations of the data, with $\alpha = 0.05$.

I assessed differences in diversity between all used and unused foraging plots at the 1-m and 2-m scales. Shannon Wiener and Simpson's diversity indices were calculated for all plots using PC-Ord and tested for significance using a Mann-Whitney test.

To assess in more detail how parrotbill were selectively using foraging habitat, I calculated proportional use of foraging habitat in used areas (Dodge et al. 1990). I summed the total observation time for each individual on each plant species, tree size class, and vegetation stratum in each home range and divided by the total observation time for each variable observed to get relative use. Relative availability of each variable was calculated in a similar manner by summing the availability of each variable in each home range and dividing it by the overall total. Tree size classes were converted to basal area so that comparisons between plant species would be weighted appropriately. I calculated overall availability of woody species only, since parrotbill do not forage on herbaceous vegetation. Percent cover was estimated for each vegetation strata (canopy, subcanopy, and understory) according to the Braun-Blanquet cover abundance scale (Braun-Blanquet 1932) and I used the midpoints for each cover class in the analyses. Data were initially collected in six different height tiers, but were analyzed due to statistical considerations based on three layers-canopy, subcanopy, and understory.

Once relative proportions were calculated for each parameter of use and availability, direct comparisons were made for each individual ($n = 14$) using a series of simple linear regressions. Calculating use and availability in this manner is an appropriate method for territorial species such as parrotbill because comparisons for each individual are made only across the territory or home range that each individual has access too. Each separate regression analysis was then assessed for statistical significance ($p < 0.05$). If a regression was significant, proportional use for each vegetation variable was derived by examining the slope of each regression line. Slopes greater than 1 signified use greater than availability while slopes less than one signified availability greater than use. Finally, I averaged values for use and availability across individuals to estimate percent use and availability for each plant species, height class, and tree size class (VanderWerf 1993, Pejchar 2004).

RESULTS

BIRD SURVEYS

Surveys suggest parrotbill occupy a greater portion of Manawainui than was previously documented. I estimated that 16 individuals occupied approximately 100 of the 270 ha of the forest comprising the study site (Figure 5). Maui Parrotbill occurred at densities of 0.06 birds/ha over the entire 270 hectare study site or 0.08 birds/ha over the 210 ha of forest intensively surveyed for birds and vegetation. I did not detect any juvenile parrotbill or nesting attempts in the study area. With the exception of the ʻĀkiapōlāʻau (*Hemignathus munroi*), parrotbill fledglings have a longer juvenile dependency period than many other honeycreepers and elicit frequent, loud begging calls while following foraging adults (Simon et al. 1997, Simon et al. 2000, Pejchar 2004). It is therefore unlikely that juvenile birds went undetected.

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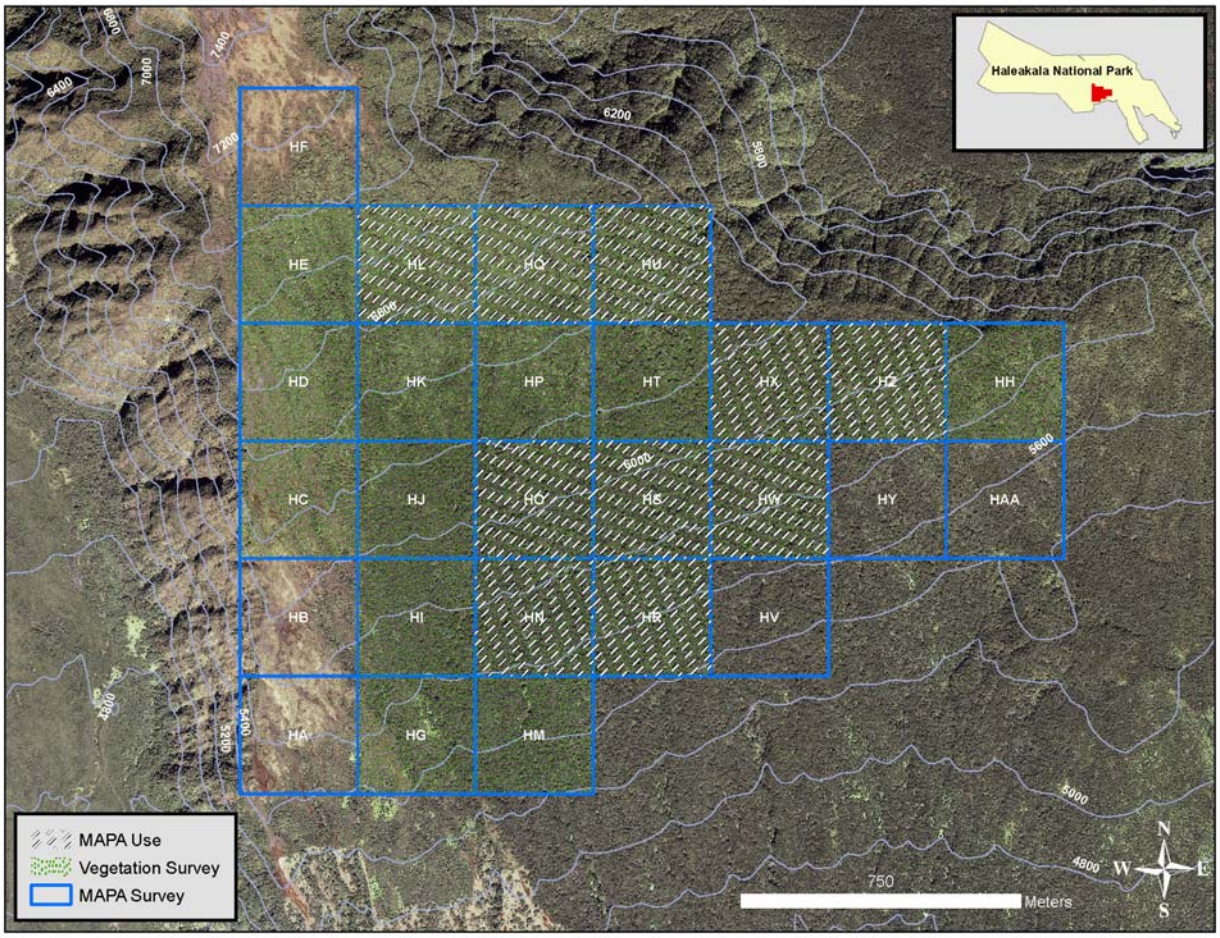


Figure 5. Distribution of Maui Parrotbill across the study site. All 10-hectare areas surveyed for birds are indicated by letters.

MACROHABITAT

Vegetation structure

I found significant differences between used and unused areas (p = 0.004, A = 0.116), based on vegetation structure (Table 3). NMS autopilot in PC-ORD selected a 2-dimensional ordination based on a low stress solution ($p < 0.05$). Most of the difference between used and unused areas was captured by axis 1 (59 %) while axis 2 captured another 30% of the variation between used and unused areas. This result was achieved after 135 iterations and had a final stress of 12.3. Plotting survey areas against axes 1 and 2 clearly segregated used and unused areas, although used areas appeared more similar to each other than unused areas (Figure 6). The number of large trees and density of subcanopy were strongly associated with the first axis, while the number of small trees and shrubs were most strongly associated with the second axis. The follow up discriminant analysis expressed these results in more detail. The standardized discriminant function coefficients associated with each variable suggest that unused areas had higher densities

of small (dbh ≥ 3-15) sized trees and shrubs. Used areas had more large trees (dbh ≥ 54cm) and denser canopy, subcanopy, and understory layers (Table 4).

Table 3. Summary statistics for vegetation structure and floristics.

Scale	Statistic	Vegetation Structure	Floristics
Macrohabitat			
10 ha	T	-3.92	-2.45
	p	**0. 004**	**0. 025**
	A	0.116	0.072
Microhabitat			
2m	F	1.39	0.78
	p	0.239	0.587
	DF	1,35	1,35
1m	F	1.56	3.97
	p	0.186	**0. 001**
	DF	1,35	1,35
0m	F	2.99	2.31
	p	0.065	**0. 026**
	DF	1,35	1,35

Macrohabitat results are for the MRPP analysis.

Microhabitat results are for the PerManova.

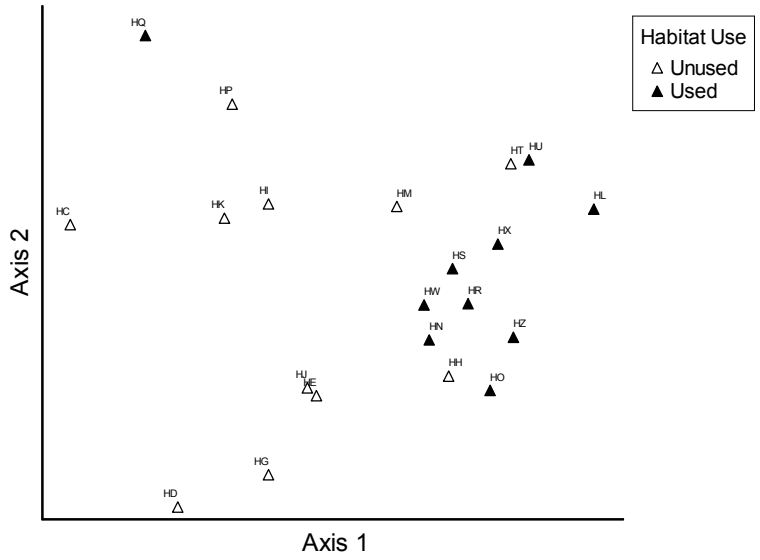


Figure 6. Final NMS ordination of 21 home ranges and habitat variables grouped by use. Each point represents a 10-hectare survey area. The degree of similarity (based on forest structure) between points is represented by the distance between each point. Significant differences between used and unused areas were evaluated using a MRPP test, see Table 3.

Table 4. Canonical discriminant functions of vegetation variables standardized by within group variances following a complete discriminant analysis.

		Group Means	
Variable	1st axis	Unused	Used
DBHLARGE	-0.671	0.84	2.48
CANTOT	0.313	0.619	0.736
UNDER	-0.532	13.18	15.34
SHRUBTLS	0.614	252.15	226.42
DBHMED	0.153	1.35	1.132
DBHSMALL	0.355	145.805	110.06
SUBCAN	-0.369	5.52	6.22

CANTOT and DBHMED values are log transformed

Floristics

A total of 55 herbaceous and woody plant species was recorded in the understory, subcanopy, and canopy in used and unused areas. A complete list of all species found in the Manawainui area with common names and taxonomic abbreviations can be found in Appendix 3. ʻŌhiʻa, was the dominant tree comprising nearly half of all tree species (48 %), followed by pūkiawe at 15%. ʻŌhiʻa, ʻōhelo, and pūkiawe were similarly dense in the shrub category, and cumulatively accounted for roughly 71% of the species. Koa accounted for less than 1% of the species surveyed in either the shrub or tree categories but was included in the analyses because the

parrotbill were known to use koa in historic times (Perkins 1903). In addition, koa is used extensively by the closest extant relative to the parrotbill, the ʻĀkiapōlāʻau.

I found significant differences between used and unused areas based on floristics ($p = 0.025$, $A = 0.072$) (Table 3). Areas without parrotbill had higher densities of ʻōhiʻa trees ($p < 0.024$), while those areas with parrotbill had higher densities of both ʻōlapa trees ($p = 0.027$), and kawaʻu trees ($p = 0.031$). Higher densities of pūkiawe shrubs ($p = 0.005$) occurred in unused areas and higher densities of ʻalani shrubs ($p = 0.012$) occurred in used areas (Table 5).

The corresponding NMS ordination selected by PC-Ord had a 2-dimensional solution with a final stress $p = 0.004$ after 78 iterations of the data. The first axis described 45 % of the variation between used and unused areas, while the second axis described 43%. The ordination graphs showed some clustering between used and unused areas although the graphs were more difficult to interpret than that for structure (Figure 7). Axis 1 was strongly correlated with the density of ʻōhiʻa, ʻōlapa, and kōlea trees and kanawao and ʻalani shrubs. Axis 2 was strongly correlated with the density of ʻōhiʻa trees and pūkiawe shrubs.

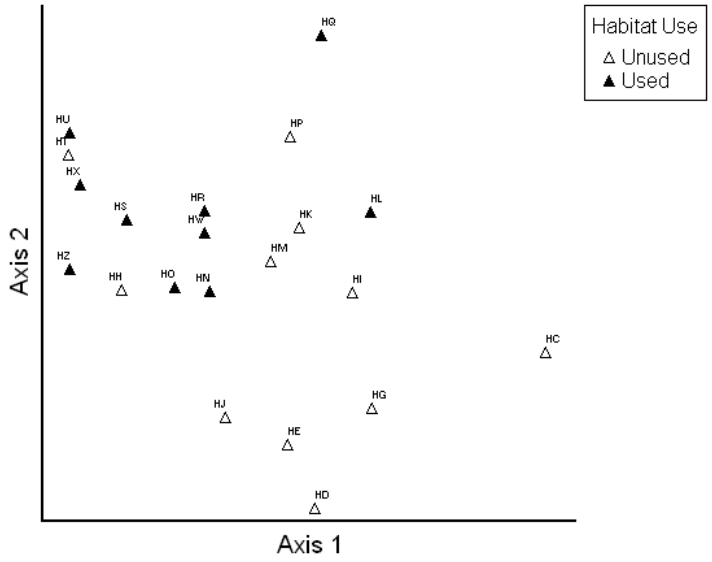


Figure 7. Final NMS ordination of 21 home ranges grouped by use. Each point represents a 10-hectare survey area. The degree of similarity (based on floristics) between points is represented by the distance between each point. Significant differences between used and unused areas were evaluated using a MRPP test, see Table 3.

Table 5. Summary of indicator species analysis results for shrubs and trees in unused (0) and used (1) 10-hectare areas.

Species	Use	Indicator value	Mean	S.Dev	*p*
Shrubs					
Metrosideros polymorpha	1	50.9	56.3	4.74	0.912
Vaccinium calycinum	0	54	56.3	4.67	0.626
Leptecophylla tameiameiae	0	77.5	59.4	6.61	**0.005**
Broussaisia arguta	1	57.5	39.5	9.17	0.052
Melicope spp.	1	73.6	48.6	8.54	**0.012**
Trees					
Metrosideros polymorpha	0	65.5	56	4.36	**0.024**
Leptecophylla tameiameiae	0	64.1	58.3	5.63	0.165
Dead	0	50.3	54.5	3.55	0.961
Cheirodendron trigynum	1	63.8	55.2	3.86	**0.027**
Vaccinium calycinum	1	50.7	57.1	7.04	0.8
Ilex anomala	1	66.7	48.1	8	**0.031**
Acacia koa	0	41.2	35.9	9.92	0.255
Myrsine spp.	1	61.9	49.1	8.82	0.096

P-values in bold indicate significance at $\alpha = 0.05$.

Diversity

Diversity of tree species was significantly higher in used areas than in unused areas for the Simpson's index only ($F = 7.75$, $p = 0.005$, df = 10, 9). There was no significant difference in species diversity between used and unused areas for trees and shrubs combined as well as for shrubs alone ($p > 0.05$) for those plants used in the MRPP tests. However, overall species diversity was higher in used areas than unused areas for both the Shannon-Wiener ($p = 0.035$) and Simpson's diversity indices ($p = 0.041$) when including all species, not just those used in the MRPP (Table 6).

Table 6. Summary statistics for diversity following a Mann-Whitney test at the macrohabitat and microhabitat scales.

	Scale					
	Macrohabitat		Microhabitat			
	10 ha		2m		1m	
	p	U	*p*	U	*p*	U
Diversity (H)	**0.035**	25	0.323	562	0.933	641
Diversity (D′)	**0.041**	26	0.323	562	0.933	641

H is Shannon Wiener index

D′ is Simpson diversity index

MICROHABITAT

A total of 22 woody plant species was recorded in the understory, subcanopy and canopy strata in 9 different home ranges. Maui Parrotbill primarily foraged on 9 different plants which included ʻākala (*Rubus hawaiensis*), ʻalani, koa, kawaʻu, kōlea, ʻōhelo, ʻōlapa, pilo (*Coprosma* spp.), and pūkiawe.

Maui Parrotbill exhibited non-random selection of foraging habitat at the two finest scales I measured (0-m and 1-m) based on floristics. Structure was not a significant factor at either scale, and overall species diversity did not differ between used and unused plots, (Table 3, Table 6).

At the 2-m scale, results of the PerManova for structure ($F = 1.39$, $p = 0.239$, df = 1, 35) and floristics ($F = 0.777$, $p = 0.587$, df = 1, 35) were non-significant ($p > 0.05$). At the 1-m scale, significant differences were detected between used and random plots based on plant species only ($F = 3.97$, $p = 0.001$, df = 1, 35). The complementary indicator species analysis however did not detect any one significant indicator species which contributed to group separation (Table 7). No significant differences for structure were observed at the 1-meter scale ($F = 1.56$, $p = 0.186$, df = 1, 35). At the finest scale, (0-m), I found significant differences between foraging sites and random sites for floristics only ($F = 2.31$, $p = 0.026$, df = 1, 35). The results of the corresponding indicator species analysis were significant for only one species; ʻōhiʻa ($p = 0.005$) which was more abundant in random than used foraging plots. No significant differences were found for forest structure at the 0-m scale ($F=2.99$, $p = 0.065$, df = 1, 35). No significant differences were detected in diversity between used and random plots at either the 1-m or 2-m scale for either diversity index using a significance level of $\alpha = 0.05$.

Table 7. Summary of indicator species analysis results for trees at the 1-m scale.

Species	Maxgrp Value	Indicator value	Mean	SD	*p*
Acacia koa	1	13.9	6.6	2.45	0.052
Alyxia oliviformis	0	2.8	2.8	0.04	1
Broussaisia arguta	0	2.8	5.4	2.58	1
Cheirodendron trigynum	1	32.1	24.4	4.18	0.088
Clermontia grandiflora	0	2.8	2.8	0.04	1
Coprosma spp.	0	16	19.4	3.76	1
Dead	0	8.7	9.1	3.2	0.713
Ilex anomala	1	11.6	7.3	2.88	0.197
Labordia venosa	1	2.8	2.8	0.04	1
Leptecophylla tameiameiae	0	6.9	10.7	3.34	1
Melicope spp.	0	16.2	11.7	3.22	0.185
Metrosideros polymorpha	0	27.2	18.6	3.99	0.066
Myrsine lessertiana	1	7.4	7.4	2.93	0.683
Rubus hawaiensis	1	11.1	10.1	3.08	0.472
Tetraplasandra oahuensis	1	2.8	2.8	0.04	1

Significance was evaluated at $\alpha = 0.05$.

I collected 32 foraging observations for an estimated 14 individuals in 8 different home ranges with a mean observation time of 380.63 seconds ± 301 SD for each observation. Parrotbill utilized koa, ʻōlapa, ʻalani and ʻākala in greater proportion than their availability throughout the home ranges ($p < 0.05$) (Table 8). Parrotbill foraged on ʻōlapa 23% of the time, koa and ʻākala 10% of the time each, and ʻalani 1% of the time (Figure 8). Plants used in proportion to their relative abundance were kawaʻu, pilo, pūkiawe, kōlea, and ʻōhelo. Standing dead trees were not utilized at all, despite their availability (11%) throughout the birds' home ranges. Parrotbill frequently excavated and gleaned invertebrates from dead wood and bark (Appendix 5).

The regression results for use versus availability of the three main height tier classes (canopy: 5-12m, subcanopy: 2-5m, and understory: 0-2m) were all significant ($p < 0.05$) with the subcanopy and canopy used more than expected, and the understory used less than expected based on availability. Parrotbill foraged at a mean height of 4.6m ± 2.24 SD and selectively foraged in the subcanopy and canopy vegetation layers, spending 41% of the time in the subcanopy and 39% of the time in the canopy (Figure 8). Birds foraged less than expected in the understory layer (Table 8).

The regression results for the analyses of use and availability for tree size class were significant ($p < 0.05$) for both small (3-15 dbh) and medium (16-53 dbh) tree size classes. Parrotbill used small trees greater than expected based on availability, foraging on them 41% of the time and used medium trees less than expected based on availability foraging on them 43% of the time (Figure 8). Parrotbill used shrubs (0-2.9 dbh) and large trees (≥ 54 dbh) in proportion to their availability. When foraging in the canopy, parrotbill foraged on ʻōlapa, koa and kawaʻu, and foraged on ʻalani, kōlea, and pilo in the subcanopy.

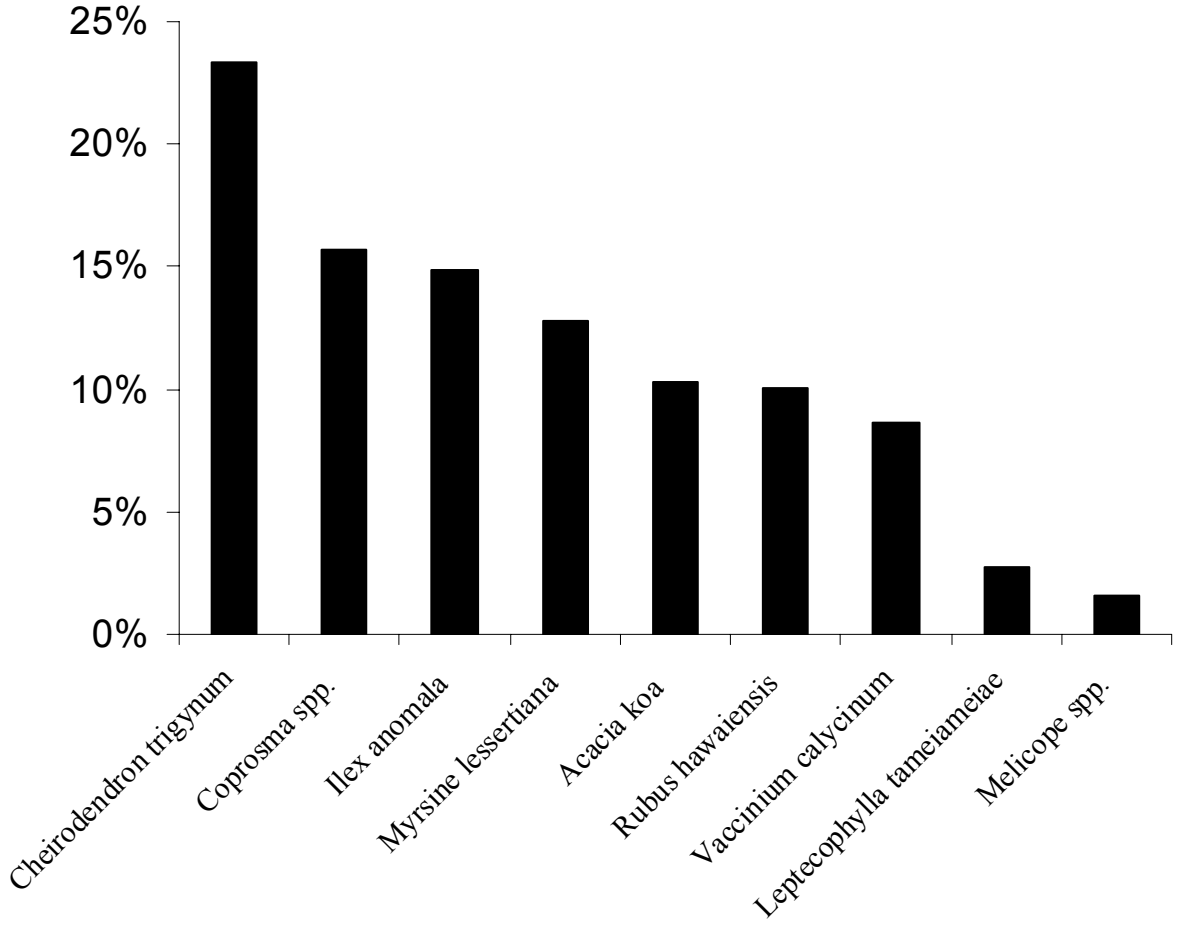
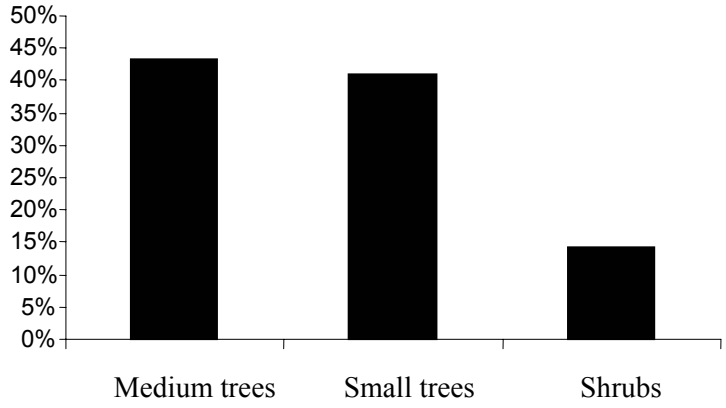


Figure 8. Mean percent time parrotbill (n = 14) spent foraging on different plant species, height tier and trees size class in 8 different home ranges in Manawainui.

Figure 8. (Continued).



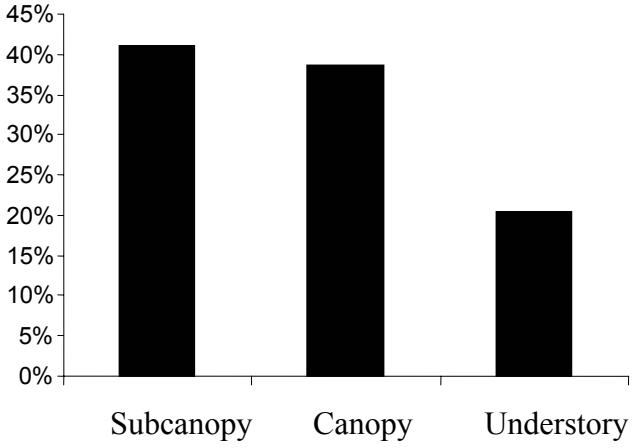


Table 8. Results of the separate regression analyses of Maui Parrotbill use vs. availability of plant species, vertical height tier, and tree size used for foraging, $n = 14$ birds.

Plant Species	**Use**	**Availability**	**Slope**	**SE**	***t***	***p***	**Conclusion**
Cheirodendron trigynum	0.234	0.039	6.51	2.10	3.09	**0.01**	U>A
Coprosma spp.	0.157	0.010	15	6.79	2.21	0.05	U=A
Ilex anomala	0.149	0.015	3.48	4.75	0.73	0.48	U=A
Myrsine lessertiana	0.128	0.013	6.98	5.42	1.29	0.22	U=A
Acacia koa	0.103	0.013	8.27	1.90	4.16	**0.00**	U>A
Rubus hawaiensis	0.100	0.001	146	52.39	2.78	**0.02**	U>A
Vaccinium calycinum	0.086	0.010	7.05	3.88	1.82	0.09	U=A
Leptecophylla tameiameiae	0.027	0.023	0.35	1.07	0.33	0.75	U=A
Melicope spp.	0.016	0.015	1.65	0.74	2.23	**0.04**	U>A
Metrosideros polymorpha	0.000	0.749	-	-	-	-	-
Dead	0.000	0.107	-	-	-	-	-
Vertical Height Tier*							
Subcanopy	0.410	0.209	1.84	0.53	3.46	**0.00**	U > A
Canopy	0.385	0.134	2.72	0.57	4.74	**0.00**	U > A
Understory	0.205	0.595	0.329	0.14	2.29	**0.04**	U < A
Upper Canopy	0.000	0.062	-	-	-	-	-
Tree Size Class**							
Medium trees	0.434	0.425	0.967	0.21	4.55	**0.00**	U < A
Small trees	0.411	0.157	2.65	0.68	3.88	**0.00**	U > A
Shrubs	0.143	0.013	6.72	4.94	1.36	0.20	U = A
Large trees	0.011	0.405	-	-	-	-	-

* Understory = 0-2m, Subcanopy 2-5m, Canopy 5-12m, Upper Canopy 12-25m

** Shrubs 0-2.9 dbh, small trees 3-15 dbh, medium tress 16-53 dbh, large trees, ≥ 54 dbh.

Use (U) and availability (A) are relative proportions, availability is the mean value for basal area of each species, and use is the mean value of foraging time. Significant regressions with slopes greater than one signify use greater than availability. Slopes less than one signify use less than expected.

DISCUSSION

MACROHABITAT

Maui Parrotbill showed strong associations with specific floristic and structural characteristics of wet forest and selected habitat non-randomly for both forest structure and plant floristics at the macrohabitat (home range) scale. Compared to unused areas, used areas contained more mature, well developed forest with a higher density of large trees, greater canopy density, subcanopy, and understory layers. Floristically, parrotbill preferred areas with higher densities of ʻōlapa, kawaʻu, and ʻalani. Overall species diversity also was significantly higher in used areas. Unused areas had higher densities of shrubs particularly pūkiawe and higher densities of small trees, particularly ʻōhiʻa. Based on this data set, koa was not a significant indicator species of parrotbill use in either used or unused areas at the macrohabitat scale. In fact unused areas had greater densities of koa than used areas. However, this does not preclude the importance of koa at the microhabitat scale, see below.

These data suggest that at the macrohabitat scale, parrotbill are selecting habitat in well developed native forest, with high species diversity and are avoiding areas with dense small-stature trees and shrubs. Diverse forest structure and species composition may serve as proximate cues for home range use. Well developed forest may reflect a need for large mature trees for nesting, singing/song posts, protection from harsh windward showers, as well as a proxy for habitat with ample foraging opportunities.

Previous researchers have noted parrotbill utilize the canopy and subcanopy trees for nesting (Lockwood et al. 1994, Simon et al. 1997) and forage primarily in the understory and subcanopy layers (Mountainspring 1987, Simon et al. 1997), indicating the importance of all three vegetation strata for this species. Parrotbill may also assess home range areas indirectly for food and/or nesting resources by using cues such as large trees and dense vegetation as correlates of prey abundance or nesting habitat, a concept known as the structural cues hypothesis (Smith and Shugart 1987).

MICROHABITAT

At the 1-m scale, no species was a significant indicator of parrotbill foraging; suggesting birds may initially react to a suite of plant species, and not just one particular plant. This may be related to fluctuations in invertebrate abundance throughout foraging sites, as well as temporal changes associated with plant species phenology throughout the year (Swezey 1954). Selecting sites with an assortment of plant species may help to offset competition from other native and non-native insectivorous species. In montane rainforest, Maui Parrotbill are frequently sympatric with Maui ʻAlauahio, the only other primarily insectivorous honeycreeper endemic to Maui. Although I did not formally survey for ʻAlauahio, they were readily observed throughout the study site, as were two prolific non-native insectivores, the Japanese White-eye (*Zosterops japonicus*) and Japanese Bush-Warbler (*Cettia diphone*). These other insectivores however, primarily glean, rather than excavate during foraging so their dietary overlap may be minimal.

At the smallest scale (0-m), differences between used and unused plots were largely driven by the presence of ʻōhiʻa, the most abundant species in the study site. Parrotbill avoided foraging in areas of dense ʻōhiʻa. Mountainspring (1987) found similar associations.

Maui Parrotbill selectively foraged on specific plant species, tree size class and vertical height tier in Manawainui. Preferential use of these vegetation variables may reflect parrotbill morphology and behavioral ecology, foraging in areas that are energetically most profitable (MacArthur and Pianka 1966). Other researchers have found that foliar architecture of certain tree species, as well as foraging height and vegetation density can strongly influence foraging success in passerines (Robinson and Holmes 1984). Preferential use of certain plants and foraging substrates in an area may indicate greater food resource availability in that patch type (Hutto 1990). Rosenberg (1990) demonstrated that birds will allocate their foraging time between different habitat types as resource abundance levels change, selecting for the most profitable foraging areas. Thus, birds may select some plants because of the expected quantity of prey, and ignore those sites or species which are less predictable (Sipura 1999, Olsson et al. 2001).

At the microhabitat scale, I found preferential use of four plant genera in our study area, koa, ʻōlapa, ʻalani, and ʻākala. This corroborates the findings of Mountainspring (1987), who studied parrotbill on windward east Maui. At this level of analysis I found preferential use of koa, not detected at the larger macrohabitat scale. This corroborates the findings of Perkins (1903), who suggested that parrotbill preferred this canopy tree as a foraging substrate. In addition, the ʻĀkiapōlāʻau, utilizes koa extensively (Pratt et al. 2001a, Pejchar et al. 2005). Pejchar (2004) documented preferential habitat use by ʻĀkiapōlāʻau in which they selectively foraged in young koa, despite its low abundance. Evidence for preferential use of koa however, does not preclude the significance of other plant species for parrotbill foraging, as preference for foraging substrates may be seasonal and/or associated with fluctuations of prey biomass (Simon et al. 1997, Berlin et al. 2001). Olsson et al. (2001) found that preferential use of tree species by Lesser Spotted Woodpeckers (*Dendrocopos minor*) within territories over the course of one year was a direct result of prey abundance in those territories. Preferential use of trees species between years however, was a direct result of the fluctuations of one particular invertebrate which was intricately tied to the phenology of several plant species.

Parrotbill foraged on ʻākala with similar intensity as koa, despite it having the lowest availability of any of the plant species the birds utilized. ʻĀkala likely provides necessary specific arthropod food resources not sufficiently available in the other plant species. Dying or dead stems of akala are relatively soft and easy for parrotbill to excavate wood boring larvae. Simon et al. (1997) also noted the importance of ʻākala to parrotbill, particularly during the fall and winter months, although I noted the birds in this study utilizing ʻākala during the spring and summer as well. ʻĀkala was scarcely distributed throughout Manawainui and further investigation into the relevance of this plant species is needed.

Maui Parrotbill selectively foraged on small trees in the subcanopy and canopy layers, using medium trees and the understory layer less than expected. Smaller trees may allow parrotbill to rapidly search an area for potential food resources, may harbor higher quantities of invertebrates per area than larger tree size classes, and often are composed of ʻōlapa, a favored plant species. Canopy structure can also influence availability of prey as well as affect a bird's ability to detect and capture prey and to hide from predators (North et al. 1999). Fretz (2002) found that lower canopy densities resulted in lower food availability for another endangered honeycreeper, the Hawaiʻi ʻAkepa (*Loxops coccineus*).

Given that parrotbill appear to be relatively sedentary foragers, overall forest density could influence their choice of foraging sites and habitat. VanderWerf (1993), found that sites with higher foliage density were preferred by ‘Elepaio (*Chasiempis sandwichensis*), possibly because denser vegetation structure may have facilitated prey capture, or protection of birds from predators. Other researchers have noted that foliar structure, such as multi- versus single-layered leaf patterns, also may influence a bird’s ability to detect and capture prey (Robinson and Holmes 1984, Holmes 1990). They found that birds adjusted their foraging search radii according to different foliage density levels among the various vegetation strata and hypothesized that vegetation density and dispersion affected how many leaves could be searched from a given perch, influencing search patterns and time allotment. Vegetation density and stratification could similarly affect the parrotbill, a species that forages actively and deliberately, making infrequent flights among foraging patches and vertical height tier.

This study focused on attributes of foraging sites. I did not address vegetation attributes of nest site selection, an area of interest which merits further investigation. Nests for Maui Parrotbill have been primarily located in canopy ‘ōhi‘a trees (Lockwood et al. 1994, Simon et al. 1997, Simon et al. 2000) suggesting the importance of this species. While smaller trees such as ‘ōlapa may be important for foraging, as the results of this study suggest, larger trees such as ‘ōhi‘a may fill other necessary roles in the ecological niche of the parrotbill.

The combined findings of macro and microhabitat suggest parrotbill respond to habitat at different spatial scales and highlight the importance of hierarchical assessments of habitat use for this species. In Hawai‘i, at least two other insectivorous species have been shown to exhibit hierarchical habitat use. VanderWerf (1993) found foraging ‘Elepaio preferred areas with dense foliage at all but the broadest of scales measured, possibly signaling more foraging opportunities in this vegetation type. Similarly, the Hawai‘i ‘Akepa has been found to prefer areas with dense canopy, likely due to higher food availability (Fretz 2002). In a study on insectivorous bark gleaning species, Adams and Morrison (1993) found that Red-breasted Nuthatch (*Sitta canadensis*) and Brown Creepers (*Certhia americana*) needed forest stands diverse in both vegetation structure and plant species composition. They found both species avoided areas dominated by dense small trees, open canopy, as well as areas lacking understory and low overall diversity of stand structure and species composition. As in this study, birds preferred mature forest with high species diversity and greater structural variation, in order to maintain habitat requirements throughout the year.

The habitat use patterns in this study mirror those documented by other researchers (Cody 1985, Rotenberry 1985, Wiens et al. 1987); parrotbill made initial broad scale decisions based on vegetation structure, and then further refined habitat use at smaller scales based on plant species composition.

CONCLUSIONS AND RECOMMENDATIONS

This work details habitat use in Manawainui, provides information on the suitability of the area as a release site, and gives insight into the habitat requirements of Maui Parrotbill. The data from this study suggest that Maui Parrotbill already occupy the most suitable habitat in Manawainui. The unoccupied habitat in this area may lack the necessary vegetation attributes for parrotbill survival, such as dense subcanopy and canopy layers, and specific plants, as noted above. This paucity may reflect inadequate food resources and could be one reason why breeding activities were not observed during this study. The results of this research support the ideal-free distribution model of Fretwell and Lucas (1972), which assumes birds will freely select the most suitable habitat for survival and reproduction. It follows then that the "available" (i.e. unoccupied) habitat in Manawainui lacks the appropriate vegetation conditions necessary for parrotbill survival.

Based on this research, releases of Maui Parrotbill into Manawainui at this time are not recommended. Immediate recovery efforts should instead focus on alternate areas and research on habitat use. Future recovery efforts for this species should include replication of vegetation measurements and habitat use as detailed in this study. Additional research might also investigate use and availability of nesting habitat, invertebrate food resources and associated plant species, and wood quality of branches. While I did not find significant interactions of parrotbill with dead trees in this study, anecdotal observations of birds foraging on dead limbs of living trees suggest these trees may be an important foraging substrate and could be a crucial component of parrotbill habitat. Mountainspring (1987) found similar associations. It is possible senescing, rather than dead plants, may provide better conditions for certain wood boring invertebrates.

Although I found some evidence of preferential habitat use of koa, this is one avenue of research that warrants further investigation. Although koa may be relevant for Maui Parrotbill, managers should also consider additional vegetation parameters, such as adequate levels of vegetation in the understory, subcanopy, and canopy, as well as a diversity of plant species and tree size classes as mentioned above, when assessing potential release sites or initiating restoration efforts for future reintroductions of this species. Parrotbill utilize a variety of plant species for foraging which may reflect temporal changes in invertebrate abundances. Thus maintaining forest diversity may be crucial to supplying adequate invertebrate food resources throughout the year.

Recovery efforts for the Maui Parrotbill would greatly benefit from systematic collection of data and hypotheses testing in response to well defined questions. Future research should include the following:

- Quantitative assessments of nesting and foraging habitat before, during, and after reintroduction/restoration efforts.
- Comparative assessments of foraging habitat, prey abundance, and territory size.
- Comparative assessments of foraging habitat for male, female and juvenile birds.
- Assessments of invertebrates and associated plant species throughout the year.

- Investigation into the potential impacts of non-native mammals, birds, and parasitoids on invertebrate prey species.
- Exploration of alternate release sites, and habitat restoration as necessary.
- Out-planting a diversity of plant species particularly ʻākala, ʻalani, kanawao, kawaʻu, koa, kōlea, ʻōlapa, and pilo in forest restoration efforts.

Habitat and food resource use are important avenues of research that have been little explored, but are necessary to further elucidate important limiting factors for this species. It is shortsighted to think that a species can be recovered or protected without an understanding of habitat and dietary requirements. Management of habitat in Hawaiʻi is frequently cited as a primary objective for numerous species, yet in many cases little is known of a species' actual habitat needs. Effective habitat management of existing areas and effective restoration of new areas can only be achieved by an in depth understanding of avian habitat requirements.

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APPENDICES

Appendix 1: All areas surveyed for vegetation and Maui Parrotbill (MAPA) in Manawainui.

MAPA Present	Number of MAPA	Sex	X	Y	Home range ID
N	0		798558	2291307	HC
N	0		798558	2291623	HD
N	0		798558	2291939	HE
N	0		798874	2290674	HG
N	0		798874	2290991	HI
N	0		798874	2291307	HJ
N	0		798874	2291623	HK
Y	1	U	798874	2291939	HL
N	0		799191	2290674	HM
Y	2	M,F	799191	2290991	HN
Y	2	M,U	799191	2291307	HO
N	0		799191	2291623	HP
Y	2	M,F	799191	2291939	HQ
Y	2	M,F	799507	2290991	HR
Y	1	M	799507	2291307	HS
N	0		799507	2291623	HT
Y	2	M,F	799507	2291939	HU
Y	1	M	799823	2291307	HW
Y	1	M	799823	2291623	HX
Y	2	M,F	800139	2291623	HZ
N	0		800455	2291307	HH

The size of each survey area was set at 10 hectares. Sexes of individuals are as follows: M=male, F=female, U=unknown sex. X and Y coordinates represent the center of each home range.

Appendix 2: All 0.04-ha vegetation plots used in the habitat analyses and corresponding UTM coordinates

Plot	Home Range	X Coordinate	Y Coordinate
HC1	HC	798580.98	2291302.02
HC2	HC	798602.15	2291340.14
HC3	HC	798553.56	2291237.08
HC4	HC	798603.43	2291258.64
HC5	HC	798554.74	2291356.25
HD1	HD	798517.91	2291646.85
HD2	HD	798556.94	2291653.78
HD3	HD	798585.38	2291667.3
HD4	HD	798511.61	2291601.9
HD5	HD	798581.54	2291573.78
HE1	HE	798531.44	2292009.48
HE2	HE	798525.62	2291879.61
HE3	HE	798593.59	2291926.5
HE4	HE	798550.45	2291949.67
HE5	HE	798623.91	2291996.31
HG1	HG	798913.18	2290608.94
HG2	HG	798914.37	2290745.46
HG3	HG	798823.14	2290599.62
HG4	HG	798939.43	2290642.97
HG5	HG	798865.12	2290607.18
HH1	HH	800520.46	2291326.15
HH2	HH	800406.84	2291299.03
HH3	HH	800421	2291259.22
HH4	HH	800396.6	2291339.15
HH5	HH	800500.73	2291233.6
HI1	HI	798920.64	2291003.66
HI2	HI	798860.45	2290956.12
HI3	HI	798883.74	2290994.17
HI4	HI	798822.2	2290940.51
HI5	HI	798902.32	2290918.73
HJ1	HJ	798910.91	2291290.08
HJ2	HJ	798845.45	2291282.42
HJ3	HJ	798910.33	2291379.04
HJ4	HJ	798838.56	2291251.22

Plot	Home Range	X Coordinate	Y Coordinate
HJ5	HJ	798910.43	2291228.92
HK1	HK	798906.96	2291583.31
HK2	HK	798820.57	2291664.74
HK3	HK	798950.52	2291605.96
HK4	HK	798805.18	2291700.05
HK5	HK	798864.58	2291692.15
HL1	HL	798913.73	2291895.61
HL2	HL	798917.39	2292014.03
HL3	HL	798856.72	2291953.37
HL4	HL	798805.98	2291923.9
HL5	HL	798872.74	2291876.1
HM1	HM	799245.29	2290722.34
HM2	HM	799258.69	2290653.59
HM3	HM	799116.54	2290726.96
HM4	HM	799243	2290627.39
HM5	HM	799199.49	2290720.16
HN1	HN	799200.96	2291042.25
HN2	HN	799182.67	2290946.39
HN3	HN	799265.69	2290912.63
HN4	HN	799149.25	2291030.4
HN5	HN	799212.43	2291006.93
HO1	HO	799240.38	2291235.7
HO2	HO	799181.39	2291307
HO3	HO	799267.5	2291333.51
HO4	HO	799121.55	2291266.98
HO5	HO	799239.01	2291274.72
HP1	HP	799119.41	2291549.54
HP2	HP	799224.68	2291677.64
HP3	HP	799214.43	2291577.35
HP4	HP	799183.24	2291620.11
HP5	HP	799140.84	2291649.33
HQ1	HQ	799262.72	2291985.18
HQ2	HQ	799179.01	2292010.87
HQ3	HQ	799208.82	2291870.65
HQ4	HQ	799232.19	2291910.06
HQ5	HQ	799266.02	2291954.45
HR1	HR	799446.07	2290913.03

Plot	Home Range	X Coordinate	Y Coordinate
HR2	HR	799482.09	2290964.55
HR3	HR	799569.48	2290947.29
HR4	HR	799484.63	2290917.58
HR5	HR	799497.71	2291019.17
HS1	HS	799468.18	2291253.42
HS2	HS	799470.82	2291375.23
HS3	HS	799574.5	2291344.72
HS4	HS	799558.62	2291241.82
HS5	HS	799491.15	2291296.02
HT1	HT	799506.41	2291616.13
HT2	HT	799564.22	2291553.67
HT3	HT	799491.86	2291697.89
HT4	HT	799504.93	2291579.67
HT5	HT	799446.88	2291638.08
HU1	HU	799466.95	2291866.27
HU2	HU	799432.9	2291900.5
HU3	HU	799569.44	2291968.86
HU4	HU	799585.65	2291924.71
HU5	HU	799540.92	2291884.92
HW1	HW	799802.07	2291330.37
HW2	HW	799843.21	2291305.25
HW3	HW	799891.3	2291345.25
HW4	HW	799805.37	2291360.32
HW5	HW	799821.25	2291237.54
HX1	HX	799865.13	2291634.97
HX2	HX	799765.29	2291566.1
HX3	HX	799766.87	2291680.13
HX4	HX	799808.42	2291665.44
HX5	HX	799812.96	2291632.79
HZ1	HZ	800096.28	2291656.67
HZ2	HZ	800132.16	2291661.03
HZ3	HZ	800215.7	2291615.51
HZ4	HZ	800176.53	2291602.08
HZ5	HZ	800069.16	2291562.52

Appendix 3: Species list and taxa codes for herbaceous and woody plant taxa found in Manawainui.

Taxon Code	Taxon	Common Name
Acakoa	*Acacia koa*	koa
Ageade	*Ageratina adenophora*	pamakani
Alyoli	*Alyxia oliviformis*	maile
Astspp	*Astelia species*	pa'iniu
Broarg	*Broussaisia arguta*	kanawao
Carspp	*Carex species*	
Chetri	*Cheirodendron trigynum*	ʻōlapa
Cibspp	*Cibotium species*	hapuu
Clearb	*Clermontia arborescence*	oha wai
Clegra	*Clermontia grandiflora*	oha wai
Copern	*Coprosma ernodeoides*	kukaenene
Copfol	*Coprosma foliasa*	pilo
Copmon	*Coprosma montana*	pilo
Copoch	*Coprosma ochracea*	pilo
Copspp	*Coprosma species*	pilo
Cyakun	*Cyanea kunthiana*	ha ha
Cyaspp	*Cyanea aculeataflora*	ha ha
Cyrspp	*Cyrtandra species*	moa
Dead	*Dead anything*	
Desnub	*Deschampsia nubigena*	
Dicsp	*Dicranopteris species*	uluhe
Dodvis	*Dodonea viscosa*	aalii
Elapho	*Elaphoglossum*	
Pepspp	*Peperomia species*	ala'ala wai nui
Hedter	*Hedyotis terminalis*	manono
Hollan	*Holcus lanatus*	
Hyprad	*Hypochaeris radicata*	hairy cats ear
Ileano	*Ilex anomala*	kawaʻu
Korthalsella	*Korthalsella*	hulumoa
Labven	*Labordia venosa*	kamakahala
Leptam	*Leptecophylla tameiameiae*	pūkiawe
Lycspp	*Lycopodium species*	
Lysrem	*Lysimachia remyi*	kolokolo
Macspp	*Machaerina species*	uki
Melclu	*Melicope clusiifolia*	ʻalani
Melorb	*Melicope orbicularis*	ʻalani
Melspp	*Melicope species*	ʻalani
Metpol	*Metrosideros polymorpha*	ʻōhiʻa
Myrema	*Myrsine lessertiana (emarginata variety)*	kōlea
Myrles	*Myrsine lessertiana*	kōlea

Nergra	*Nertera granadensis*	makole
Orefur	*Oreobolus furcata*	
Physpp	*Phyllostegia species*	ulihi
Pitcon	*Pittosporum confertiflorum*	hoawa
Psymau	*Psychotria mauiensis*	kopiko
Rubhaw	*Rubus hawaiensis*	ʻākala
Scaspp	*Scaevola species*	naupaka
Smimel	*Smilax melastomifolia*	hoi kuahiwi
Stekam	*Stenogyne kamehamehame*	mohihi
Stespp	*Stenogyne species*	mohihi
Tetoah	*Tetraplasandra oahuensis*	ohe
Uncunc	*Uncinia unicinata*	
Vaccal	*Vaccinium calycinum*	ʻōhelo
Vacden	*Vaccinium dentatum*	ʻōhelo
Vacret	*Vaccinium reticulatum*	ʻōhelo

Appendix 4: Summary table for habitat variables measured in 21 ten hectare areas in Manawainui.

Floristics		Used	(n = 10)		Unused	(n =11)
Plant species or genus[1]	Mean	StDev	SE	Mean	StDev	SE
Acakoa	29.5	54.7	17.3	290	493	149
Broarg	3383	2766	875	1309	2708	816
Chetri	1020	418	132	829	683	206
Melspp	3204	2141	677	1177	2005	604
Leptam	3179	2008	635	10321	7758	2339
Copspp	1713	667	211	783	942	284
Ileano	121	100.9	31.9	73.2	121.1	36.5
Myrspp	969	945	299	295	488	147
Metpol	9137	6223	1968	9953	6502	1961
Dead	363	144.6	45.7	366.8	231.8	69.9
Rubhaw	632	1108	350	107.7	199	60
Vaccal	6400	4380	1385	7463	5561	1677
Physiognomy						
Elevation in meters	1850.2	102.6	32.4	1854.8	133.1	40.1
Percent slope	21.26	6.44	2.04	22.09	9.03	2.72
Percent Canopy Cover	70.8	9.33	2.95	67.68	14.22	4.29
Percent Ground Cover	62.9	13.28	4.2	59.73	10.14	3.06
Canopy Height in meters	8.092	2.572	0.813	9.507	3.22	0.971
Medium trees (stems/ha)	388.7	238.8	75.5	590.9	204.6	61.7
Small trees (stems/ha)	2752	777	246	3645	1525	460
Large trees (stems/ha)	62	29.27	9.26	20.91	29.22	8.81
Shrubs (stems/ha)	5660	2586	818	6304	3175	957
Canopy density index	5.56	1.192	0.377	5.136	2.481	0.748
Understory density index	15.34	4.45	1.41	13.182	2.875	0.867
Subcanopy density index	6.62	0.373	1.18	5.52	1.12	0.333

[1] Density expressed as stems/ha. Only those woody plants species that occurred in > 5% of the sampling units, or that were likely to be used by Maui Parrotbill are shown.

Appendix 5: Count of all foraging behaviors for Maui Parrotbill by substrate and plant species, *n* = 60 observations. Includes observations not used in the microhabitat foraging analyses.